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Abstract

Ecosystem models are currently one of the most powerful approaches used to project and analyse the consequences of anthropogenic and climate-driven changes in food web structure and function. The modeling community is however still finding the effective representation of microbial processes as challenging and lacks of techniques for assessing flow uncertainty explicitly. A linear inverse model of the Bay of Biscay continental shelf was built using a Monte Carlo method coupled with a Markov Chain (LIM-MCMC) to characterize the system's trophic food-web status and its associated structural and functional properties. By taking into account the natural variability of ecosystems (and their associated flows) and the lack of data on these environments, this innovative approach enabled the quantification of uncertainties for both estimated flows and derived food-web indices. This uncertainty assessment constituted a real improvement on the existing Ecopath model for the same area and both models results were compared.

Our results suggested a food web characterized by main flows at the basis of the food web and a high contribution of primary producers and detritus to the entire system input flows. The developmental stage of the ecosystem was characterized using estimated Ecological Network Analysis (ENA) indices; the LIM-MCMC produced a higher estimate of flow specialization (than the estimate from Ecopath) owing to better consideration of bacterial processes. The results also pointed to a detritus-based food-web with a web-like structure and an intermediate level of internal flow complexity, confirming the results of previous studies. Other current research on ecosystem model comparability is also presented.

Key words: ecosystem; food web; Ecological Network Analysis indices; linear inverse model; Bay of Biscay

I. Introduction

Natural systems are known to demonstrate strong spatial and temporal variability (Frontier et al., 2008), however scientists encounter problems relating to the quantification of uncertainty when trying to represent an environment at a particular point in space or time, especially in trophic modeling. Several methods have been developed to assess the food-web properties of an ecosystem; linear inverse models using a Monte Carlo method coupled with Markov Chain (LIM-MCMC; Van der Meersche et al., 2009; van Oevelen et al., 2010) are an innovative technique for quantifying uncertainty in both flows and indices relating to the structural and functional properties of an ecosystem (Niquil et al., 2012). The idea of using a LIM-MCMC to describe each flow in terms of a range of possible values rather than a single value, was first proposed by Donali et al. (1999) and developed further in more recent studies (Leguerrier, 2005; Kones et al., 2006). The LIM-MCMC approach makes it possible to take into account flow variability, which is usually the result of uncertainties in observational data (van Oevelen et al., 2010; Niquil et al., 2012). The uncertainty is integrated into the model by defining minimum and maximum boundaries for each flow. Because it takes into account uncertainty in flow, the method also permits a distinction to be drawn between local data (from the period or region for which a solution was tested) and data from a different but related ecosystem. This new approach enables minimum and maximum flow values and average estimates with standard deviations to be computed on the basis of a given number of flow solutions; a similar approach can be used with indices related to the structural and functional properties of an ecosystem (van Oevelen et al., 2010; Niquil et al., 2012).

Linear inverse methods are also well suited to describing eco-physiological processes operating in the microbial food web, such as plankton excretion and bacterial uptake of dissolved organic carbon. This is important because there is also consensus amongst the scientific community on the urgent need for comprehensive incorporation of microbial

processes into models in order to provide a holistic understanding of ecosystem structure and function, from prokaryotes to top predators (Davidson, 1996; Li et al., 2011; Saint-Béat, 2012). The LIM approach has been used quite frequently in aquatic plankton ecology (e.g., Vézina and Pace, 1994; Vézina and Savenkoff, 1999; Niquil et al., 2001; Marquis et al., 2007) but despite its advantages it has rarely been applied to larger marine ecosystems, an exception being a study of the Gulf of St Lawrence (Savenkoff et al., 2007; Rioual, 2012).

The Marine Strategy Framework Directive (MSFD - Directive 2008/56/EC) established criteria and associated indicators (MSFD - Decision 2010/477/EC) for what the MSFD refers to as "Good Environmental Status" (GES) in European Waters. Evaluation of the initial list revealed that it was inadequate for determining whether a marine food web had reached GES (Rombouts et al., 2013). A list of nine food web indicators which would better capture food web characteristics (i.e., structure, functioning and dynamics), and thus complement the existing GES definition, was submitted to the OSlo and PARis (OSPAR) Intersessional Correspondence Group For Coordination Of Biodiversity Assessment and Monitoring (ICG-COBAM; International Council for the Exploration of the Sea [ICES], 2013; Niquil et al., 2014b). Two of these indices are related to the concept of fishing down the food-web (Pauly et al., 1998) by measures of size (Large Fish Index) or mean trophic level of predatory fishes (Marine Trophic Index). Two other are related to trophic guilds, either composed of fish or plankton. The Ecological Network Analysis indices were among these candidate indicators and are currently being assessed, in order to look for holistic and functional indicators.

Ecological network analysis (ENA; Ulanowicz, 1986) was developed to identify holistic structural and functional properties which are not directly observable and can only be detected by analysis of within-system interactions (Fath et al., 2007). The main challenge for ENA is to capture an ecosystem's entire food web in terms of a limited number of indices. Previous research has suggested that the values of ENA indices varied according to the pressures on a

given ecosystem, and among habitats (Patrício et al., 2004; Dame and Christian, 2007; Coll et al., 2009; Pranovi and Link, 2009; Baeta et al., 2011; Niquil et al., 2014a). ENA index values derived from a LIM-MCMC include a measure of the uncertainty of the estimates, unlike those derived from other over-constrained models. Information about uncertainty can be crucial as some changes in the variance of such indices may reflect an important shift in the trophic status of an ecosystem, e.g., changes in the Baltic Sea (Tomczak et al., 2013) and, more recently, changes in the Ionian Sea in response to climate changes (Niquil et al., submitted).

The present work was methodological; our focus was on documenting a non-familiar modeling approach when considering large marine ecosystems. The LIM-MCMC method would address two of the main weaknesses typical of food web modeling, i.e., the model should include an uncertainty assessment and provide a better representation of low-trophic-level processes. A LIM-MCMC was set up for the Bay of Biscay continental shelf. The full presentation of steps and issues related to the LIM-MCMC construction and uncertainty analysis were provided. Then, the food web status of the Bay of Biscay and its structural and functional properties were characterized through the calculation of a range of ENA indices. Finally, ecological conclusions derived from the LIM-MCMC were compared with those obtained with a pre-existing Ecopath model of the same ecosystem (Lassalle et al., 2011).

2. Material and Methods

2.1. Study area

The Bay of Biscay is a Gulf of the North-East Atlantic Ocean, located off the west coast of France and the northern coast of Spain (Figure 1) between 48.5°N and 43.5°N; 008°W and 003°W. This ecoregion is subject to a wide variety of environmental processes such as coastal upwelling, coastal run-off and river plumes, seasonal currents, eddies, internal waves and tidal fronts (Planque et al., 2004). Five main rivers supply fresh water to the sea: the Loire, the Garonne–Dordogne, the Adour, the Vilaine and the Charente; these rivers modulate the salinity of the plume regions. All these processes influence the biological communities of the Gulf, especially the plankton communities, and affect the functioning of the whole food-web (Varela, 1996; Lampert, 2001). The Bay of Biscay supports a multifleet fishery, primarily operated by French and Spanish boats, which exploits a wide range of species using diverse types of fishing gear (Rochet et al., 2012). For this study we considered only ICES divisions VIIIa and VIIIb (ICES; www.ices.dk), between the 30m and 150m isobaths, giving a total surface area of 102,585 km².

2.2. Model complexity

Some of the input parameters for the LIM-MCMC were taken from the Ecopath model (diet composition, pedigrees, Production/Biomass (P/B) ratios). These parameters were used to define compartment interactions, mass balances and some flows constraints (e.g., production constraints).

The first step in compartment model construction is to define the protagonists of the various interactions and how they are aggregated into compartments (Johnson et al., 2009; Niquil et al., 2012). The species composition of our model (Tables 1 and 2) varied very little from that presented by Lassalle et al. (2011; supplementary material); the main differences between the

two models are structural. In this study the number of compartments was reduced by a factor of roughly two, from 32 to 18 (Tables 1 and 2). The aim of this simplification of structure was threefold: (i) to describe and constrain the flows without applying the same constraints to different compartments; (ii) to characterize all compartments with the same precision; there was not sufficient ecological data from all the 32 Ecopath compartments to include them as stand-alone compartments in the LIM; and (iii) to achieve a sensible balance between the time required to run simulations and the level of detail in which flow values were explored.

Ecopath compartments which were mono-specific, and for which there was either (i) insufficient physiological data, or (ii) which occupied the same trophic position in the upper food web (i.e., the five marine mammal compartments, the two seabird compartments and two cephalopod groups), were combined (Tables 1 and 2). The Ecopath model used four compartments for demersal fish on the basis of their trophic ecology; we chose to distinguish strictly benthivorous demersal fishes from other demersal species. The Ecopath model used five mono-specific compartments to represent small pelagics; in the LIM-MCMC pelagic fishes were separated into two groups based on feeding habits, pelagic piscivorous and strictly pelagic planktivorous (Table 2). Necrophageous and carnivorous invertebrates were aggregated on the basis of the reduced number of invertebrate species with a necrophageous diet in the LIM-MCMC. In the LIM-MCMC, the other four invertebrate compartments of the Ecopath model were aggregated on the basis of the commonly used dichotomy between deposit and suspension invertebrate feeders. The two size-classes of phytoplankton were considered together. Discards, commonly regarded as dead organisms, were not distinguished from detritus (i.e., particulate organic matter, POC). Finally the LIM-MCMC included an additional dissolved organic carbon (DOC) group (Tables 1 and 2). The second step in defining the network topology, after the groups had been established, was the listing of all the

143 possible flows between compartments and at the system margins (see Table S1 in
144 Supplementary Material).
145
146 2.3. General principles and parameterization
147 The food-web model used was a linear inverse model based on the Monte Carlo Markov
148 Chain (LIM-MCMC; Van den Meersche et al., 2009; van Oevelen et al., 2010). It was defined
149 by a combination of mass-balance equations (and potential *in situ* measures of flow expressed
150 as complementary equations) and inequalities which constrain flow values. In most cases
151 constraints were based on the eco-physiology of the species making up the model
152 compartments (Niquil et al., 2012).
153 The linear equalities describing the system were typically expressed as a matrix calculation:
154 $$A \bullet r = b \qquad \text{(Eq.1)}$$
155 where A is the matrix of coefficients, r the vector of possible flows and b the vector of
156 equality results.
157 The solution is based on finding the vector r for which the equations are valid.
158 The system of equalities is underdetermined, so in most cases complementary inequalities
159 were added to constrain the flows. The system of linear inequalities can be written as:
160 $$G \bullet r \geq h \qquad \text{(Eq.2)}$$
161 where G is the matrix of coefficients (inequality relationships) and h the vector of inequality
162 values. These constraints reduced the area of the solution space to a polytope. Following this a
163 mirror of the Monte-Carlo-Markov Chain technique (Van den Meersche et al., 2009) was
164 applied to explore the polytope and describe all possible solutions.
165
166 2.3.1. Equalities

In this model, equalities were only described by mass-balance equations (Table S2); no nominal flow values were entered in the model to take into account the uncertainty in field data collected from an ecosystem. Model equalities captured the fact that, for each compartment considered in the model, input flows (i.e., imports or consumption) were equal to output flows (i.e., exports, production, respiration, production of detritus or egestion, and in some cases, excretion). The model assumed an intrinsic steady-state system in which biomasses were not changing and net migration (difference between emigration and immigration) was equal to zero or negligible on an annual scale. Mortality in the model was mainly due to predation and exports by fisheries, natural mortality other than predation, such as disease, was considered negligible in comparison with mortality by predation or fishing.

Eighteen mass-balance equations, one per compartment (Table S2), were set up in matrix form (matrix **A**). There were as many rows as there were mass-balance equations (m = 18) (Table S2). The columns of the matrix represent the flows; there were as many columns as there were flows (n) in the food web (Table S1). The vector of equality results b (m x 1) thus contains the right-hand sides of the mass-balance equations. Inverse methodology was then used to calculate a vector r (n x 1) with as many elements as there were columns in **A**. Vector r represents the flows that, when multiplied by **A**, approximates the vector b (Eq. 1). The diet content matrix from the Ecopath model was used to determine coefficients for output predation flows in these equations. Additional predation flows were integrated (e.g., Marquis et al., 2007; Saint-Béat et al., 2013) on the same basis, especially those relating to consumption of bacteria in the system, roughly restricted to microzooplankton in the Ecopath model (Table 1 and Table S2 in Supplementary Material).

2.3.2. Inequalities

Constraints were added to the model, i.e., flow estimates were constrained between pre-defined minima and maxima (Table S3). Inequalities were included by filling a matrix **G** of *c* x *n* where *c* was the number of inequalities added to the model and *n* the number of possible flows, with negative or positive coefficients between 0 and 1 (Eq. 2). The vector *h* for the inequalities (*c* x 1) formed the right-hand side of the inequality relationship and thus had as many elements as there were rows in **G**.

Respiration

Bacterial respiration was constrained by setting minimum and maximum values for DOC uptake by bacteria (Vézina and Savenkoff, 1999). Phytoplankton respiration was limited to 5 to 30% of gross primary production (GPP) in accordance with constraints set out by Vézina and Platt (1988). The lower boundary for respiration in zooplankton compartments was defined as 20% of their ingestion, in defining the upper boundary, the sum of their respiration, excretion and egestion was assumed to be less than 75% of their ingestion (Vézina and Pace, 1994). Respiratory constraints for meiofauna and benthic invertebrates were derived from van Oevelen et al. (2006) (Table S3).

Excretion

Bacteria, phytoplankton and micro- and meso-zooplankton excrete or exude carbon to the DOC compartment (Riemann et al., 1990). Because there is no precise method of estimating the transformation of particulate detritus into DOC (Pace et al., 1984), this constraint was not considered in the present model. Excretion flows for the four compartments mentioned above were constrained according to Vézina and Platt (1988) and Vézina and Savenkoff (1999) (Table S3).

Egestion

Egestion was constrained on the basis of assimilation efficiency (AE) rates found in the literature (Vézina and Platt, 1988; Scheiffarth and Nehls, 1997; Leguerrier, 2005; van

Oevelen et al., 2006) (Table S3). AE rates were included for all compartments except cephalopods and marine mammals (low confidence or lack of information). AE is defined as the amount of carbon that is assimilated divided by the total amount of carbon ingested (∑ consumption) (van Oevelen et al., 2006):

$$AE = \frac{\sum consumption - loss\ to\ detritus}{\sum consumption} \qquad \text{(Eq.3)}$$

Production

Production estimates were obtained by multiplying the two key input parameters for the Ecopath model of the Bay of Biscay continental shelf food web, P/B ratios and biomass estimates. Inter-annual variations in compartment biomass multiplying by mean P/B ratio were used to calculate minimum and maximum production for each compartment. The biomass values for the Ecopath model were the averages of annual estimates for the period 2000–2010. The lower bound for production was equal to the P/B ratio multiplied by the lowest biomass recorded during this period and vice versa. At the time scale considered and for a given species, the variation of P/B was negligible. Thus, we did not consider the variation of P/B for the production estimation.

Gross Primary Production (GPP) was considered as an import to the phytoplankton compartment. Constraints on this flow are therefore described in the Imports section below.

Growth efficiency

Additional constraints on growth efficiencies (GEs) were added. GE is the ratio of production to ingestion, i.e., GE = Production/ Ingestion. According to Christensen and Pauly (1992), most consumer organisms have a GE between 10% and 30% (Table S3).

Import

Two main imports were considered in the present model, import to phytoplankton (GPP) and import of detritus.

240 Estimates of GPP were derived from estimates of net primary production (NPP) from four
241 Earth system models (Bopp et al., 2013): the CESM1-BGC, the GFDL-ESM2G, the GFDL-
242 ESM2M and the NorESM1-ME. These four models were selected from the range of Earth
243 system models because they gave NPP estimates similar to SeaWifs observation data for our
244 study area over the 1975-2005 period (Bopp et al., 2013). These estimates were also
245 comparable to the NPP *in situ* value entered into the Ecopath model of the Bay of Biscay
246 continental shelf. Minima and maxima were based on the 5th and 95th percentiles of model
247 estimates.

248 Detritus imports from the five main rivers flowing into the Bay of Biscay were estimated from
249 measurements of POC in estuaries (Abril et al., 2002) and mean annual river discharges
250 (www.hydro.eaufrance.fr). Lower and upper bounds were related to inter-annual variability of
251 river discharges over the 1998-2002 time period.

252 *Export*

253 Exports out of the system by commercial groups were mainly due to fishing. Estimates were
254 based on international landing statistics for ICES divisions VIIIa and VIIIb for the 1998-2002
255 period. These data were complemented by data from the relevant ICES working groups, i.e.,
256 the WGCEPH for cephalopods (ICES, 2005a) and the WGMHSA for small pelagic fish
257 (ICES, 2005b). Landings for the various exploited species in a compartment were summed.
258 Lower and upper limits were derived from landing time series.

259 Exports of detritus (sedimentation to greater depths or transport of particulate matter by
260 currents) were also considered, but no maximum or minimum constraints were applied owing
261 to lack of information.

262 *Diet composition*

263 The Ecopath model gave pedigree index values which categorized the quality of data sources
264 for the five main input parameters (biomass, P/B, consumption/biomass, diet composition,

and commercial catches) (Christensen et al., 2008). These authors associated a default confidence interval with each pedigree index value. Thus, depending of the quality of the origin input, pedigree index values of 0, 0.2, 0.5, 0.7, and 1 correspond, for diet composition, to confidence intervals of ± 80%, ± 80%, ± 50%, ± 40%, and ± 30%, respectively. The pedigree table for the Ecopath Bay of Biscay continental shelf food web model has recently been completed (Lassalle et al., 2014). Lower and upper limits for diet composition were based on the diet composition matrix of the Ecopath model and the related confidence intervals in the pedigree table.

2.4. Data used in modeling

Compartment production, import, and export data were estimated from scientific survey data (PELGAS cruises, MICRODYN, BIOMAN, and INTRIGAS surveys; Labry et al., 2002; Le Loc'h, 2004; Irigoien et al., 2009) collected during different seasons over the period 1994-2005 by the Institut Français de Recherche sur l'Exploitation de la MER (IFREMER), the AZTI-Tecnalia (a Technological Centre specialised in Marine and Food Research), and the Centre National de la Recherche Scientifique (CNRS). A full description is provided in Lassalle et al. (2011).

Fish stock data were taken from the ICES/ACFM advice report (ICES, 2004) and biomasses of fish species were estimated from annual autumn surveys of bottom-trawl catches in the Bay of Biscay (EVHOE IFREMER cruises). Pelagic fish biomasses were calculated from acoustic surveys conducted each spring in the Bay of Biscay (PELGAS IFREMER cruises).

Sea birds estimates were based on data from visual counting and identification and aerial surveys performed monthly between October 2001 and March 2002, and in August 2002, June 2003 and May 2004 (ROMER and ATLANCET surveys). Finally, data on marine mammals were obtained from (i) the July 2005 SCANS-II project (ship and aircraft surveys of

small cetaceans in the European Atlantic); (ii) repeated extensive aerial surveys at different seasons between 2001 and 2004 (ROMER and ATLANCET surveys; Certain et al., 2008), and (iii) the monitoring of marine mammals via stranding and spring shipboard observations during the PELGAS IFREMER cruises (Certain et al., 2011).

2.5. Model resolution

The mirror technique described by Van Den Meersche et al. (2009) was used to compute a multitude of solutions and quantify uncertainty around all flows. Two parameters must be defined in order to use this technique: a number of iterations to optimize the exploration (or coverage) of the polytope of solutions and a 'jump' representing the mean distance between two consecutive solutions in a randomly chosen direction. For this study one million solutions were calculated with a jump equal to 100 $kgC.km^{-2}.y^{-1}$ which corresponded to an approximation of the median of the flow values. The jump was set up in order to get a good polytope exploration and also to get better estimations of small and large flows. All simulations were performed using the MATLAB software and the algorithm developed by Vézina and Campo (Bedford Institute of Oceanography, Fisheries and Oceans, Canada), which is a translation of the R package *limSolve* (Soetaert et al., 2009).

2.6. Ecological network analysis

Ecological network analysis (ENA; Ulanowicz, 1986) was used to compute several indices to characterize the structure and function of the Bay of Biscay continental shelf food web. To facilitate comparison of our model with the Ecopath model, we calculated values for the ENA indices estimated by Lassalle et al. (2011) for the Ecopath model, namely Total System Throughput (T..), Internal Relative Ascendency (Ai/Ci), Finn Cycling Index (FCI), System Omnivory Index (SOI) and Connectance Index (CI). The T.. index computed as the sum of all

315 flows in a food web thus acts as a proxy for system activity or organization. The internal
316 relative ascendency (Ai/Ci) ratio provides a relative measure of the degree of organization of
317 a food web based only on internal flows and was directly issued from the Ecopath model.
318 Finn (1980) proposed an index of the importance of recycling activity based on the percentage
319 of flows involved in cycles. According to Ulanowicz (1986), CI and SOI values generally
320 reflect the complexity of the linkages within an ecosystem (in terms of both structure and
321 organization).

322 A LIM-MCMC MATLAB routine adapted from the one developed by Lebreton and Schartau
323 (GKSS Research Center, Geesthacht, Germany) was used to compute one ENA index value
324 for each flow solution estimated by the LIM-MCMC.

325 We also compared the Detritivory/Herbivory (D/H) ratio, calculated as the sum of flows
326 originating from detritus and DOC compartments (detritus consumption) divided by the sum
327 of flows from phytoplankton (phytoplankton consumption). The D/H ratio measures the
328 relative importance of detritivory and herbivory activity in a given system.

329

330 2.7. Analysis of flows and ENA indices

331 The general distribution of the flows estimated by the LIM-MCMC was assessed with two
332 barplots, one including all estimated flows and the second restricted to the five flows with the
333 highest mean values.

334 The structure of the food web was investigated by analyzing the input flows of the
335 compartments; input flows were only compared for compartments which were defined
336 similarly in both models. The position of Ecopath value inside or outside the range of values
337 estimated by the LIM-MCMC was assessed.

Respiration flows in the two models were also compared and cases in which the single Ecopath value fell within the range of possible values predicted by LIM-MCMC were noted.

Values for the ENA indices which were estimated in both models were also compared and the relative position of the Ecopath values analyzed.

We did not carry out any of the classic mean comparison tests because of the important size of the samples (1 million observations in the LIM-MCMC *vs.* one Ecopath reference value); the Markov-Chain used in the LIM-MCMC also meant that the independence of observations criterion was not satisfied. However, we considered instances in which the Ecopath value fell within the range estimated by the LIM-MCMC to be highly informative (and significant) even without further analysis.

348 3. Results

349 Estimates of flows from the LIM-MCMC are given in the Supplementary Material (Table S1).
350 The highest flows in the food web were mainly related to phytoplankton production,
351 consumption, sedimentation or exudation (1-10), or to bacterial and detrital processes (80-98)
352 (see Figure 2A and Table S1 in Supplementary Material). The flows with an average higher
353 than $5 \cdot 10^4$ kgC.km^{-2}.y^{-1} (Figure 2B) were: the GPP (1), $2.41 \cdot 10^5 \pm 0.5 \cdot 10^5$ kgC.km^{-2}.y^{-1};
354 the phytoplankton sedimentation (2), $1.10 \cdot 10^5 \pm 0.23 \cdot 10^5$ kgC.km^{-2}.y^{-1} and the
355 consumption of dissolved organic carbon by bacteria (98), $1.04 \cdot 10^5 \pm 0.35 \cdot 10^5$ kgC.km^{-2}.y^{-1}.

357 The two detrital groups (i.e. POC and DOC) and the phytoplankton compartment contributed
358 to 18.8%, 10.8%, and 31% of the total carbon input *via* river discharges and GPP,
359 respectively. The estimated net allochthonous input of 502.65 kgC.km^{-2}.y^{-1} of detritus was
360 low in comparison with GPP ($2.41 \cdot 10^5 \pm 0.5 \cdot 10^5$ kgC.km^{-2}.y^{-1}). Detailed compartment
361 input flows (sum of carbon entering a given compartment) are given in Figure 3. Comparison
362 of estimated compartment input flows from the LIM-MCMC and the Ecopath model revealed
363 a similar pattern, especially for first trophic level compartments; in both models there was a
364 peak of activity associated with pelagic planktivores. Graphical comparison of compartment
365 input flows for the two models (to assess whether the Ecopath estimate fell within the LIM-
366 MCMC estimated range) revealed that results were consistent for most groups; the main
367 difference was in microzooplankton input flow estimates (average values were $7.8 \cdot 10^4$
368 kgC.km^{-2}.y-1 for the LIM-MCMC and $2.8 \cdot 10^5$ kgC.km^{-2}.y^{-1} for the Ecopath model).

369 Respiration flows accounted for 86.7% of the carbon output ($2.1 \cdot 10^5$ kgC.m^{-2}.y^{-1}) of the
370 system. The contribution from bacterial respiration (29.5% of total respiration) was closely
371 followed by meiofaunal respiration (27.1%). Comparison of respiration estimates revealed
372 that half the values for respiration flow estimated with the Ecopath model lay within the range

of estimates given by the LIM-MCMC. The remaining estimates were evenly distributed, suggesting that neither model systematically over- or under-estimated respiration flow. The greatest differences in estimated respiration flow were for seabirds (LIM-MCMC: 533.44 ± 189.58 $kgC.km^{-2}.y^{-1}$; Ecopath: 16.42 $kgC.km^{-2}.y^{-1}$) and meiofauna (LIM-MCMC: $5.8 \cdot 10^4 \pm 2.61 \cdot 10^4$ $kgC.km^{-2}.y^{-1}$; Ecopath: 2000 $kgC.km^{-2}.y^{-1}$).

LIM-MCMC estimates of T.. ranged from $7.35 \cdot 10^5$ $kgC.km^{-2}.y^{-1}$ to $8.44 \cdot 10^5$ $kgC.km^{-2}.y^{-1}$. The Ecopath model estimate, $9.4 \cdot 10^5$ $kgC.km^{-2}.y^{-1}$, was above the maximum LIM-MCMC estimate (Figure 4). Estimates of internal relative ascendency, which does not include external flows (flows entering and exiting the system), were also compared. The mean internal relative ascendency from the LIM-MCMC was 0.34 ± 0.01, which was higher than the Ecopath estimate, 0.22.

The average cycling index value obtained from the LIM-MCMC was 0.13 ± 0.01, notably lower than the Ecopath estimate, 0.35. Comparison of D/H ratios revealed that the Ecopath model estimate (1.32) was within the range of LIM-MCMC estimates (0.46 – 1.84) and close to the mean LIM-MCMC estimate.

The LIM-MCMC estimate of CI was higher than the Ecopath model estimate (LIM-MCMC: 0.32; Ecopath: 0.21) while estimates of SOI were similar (LIM-MCMC: 0.19 ± 0.03; Ecopath: 0.21), see Table 4.

391 4. Discussion

392 This study is one of the first attempts to model a large exploited marine ecosystem using the
393 LIM-MCMC method. This innovative approach to modeling was developed for theoretical
394 exploration of ecological networks; it enables uncertainties to be quantified and allows
395 complex eco-physiological processes operating at the level of the food-web to be incorporated
396 into models. Interestingly, the LIM-MCMC of the Bay of Biscay continental shelf provided
397 results which confirmed and extended the findings derived from an earlier Ecopath model by
398 Lassalle et al. (2011). The estimates produced by the two models differed little with respect to
399 the flows analyzed and five ENA indices investigated, however comparison of values for
400 more ENA indices and respiration flows could reveal differences. In both the LIM-MCMC
401 and the Ecopath model (Lassalle et al., 2011) the highest flow estimate was for GPP. Lassalle
402 et al. (2011) showed that flows from primary producers were 47.5% of total system
403 throughput. High phytoplankton sedimentation and detritus production (egestion for each
404 consumer group) estimates produced by the LIM-MCMC and the high value for consumption
405 of DOC by bacteria - a process not included in the Ecopath model - confirmed that an active
406 bacterial loop played a critical role in carbon recycling and in general ecosystem functioning.
407 The convergence in estimates of the degree to which low trophic levels dominated system
408 functioning was also observed for results at the second trophic level, mainly composed of
409 bacteria and zooplankton.

410 Respiration flows constituted the main source of uncertainty in the Ecopath model
411 (Christensen et al., 2008). In contrast to the convergence between the models' estimates of
412 compartment input flows, there were differences in estimates of respiration flows for some
413 compartments. The largest differences were in estimates of respiration flows for seabirds and
414 meiofauna, with LIM-MCMC mean values 30 times higher than the Ecopath values. In the
415 LIM-MCMC presented here, respiration flows of lower trophic levels (phytoplankton,

bacteria, zooplankton, meiofauna and benthic invertebrates) were constrained by lower and upper eco-physiological boundaries; for the higher trophic levels, they were constrained indirectly by constraining physiological ratios such as GE or AE (Winberg, 1956; Vézina and Platt, 1988; Christensen and Pauly, 1992; Scheiffarth and Nehls, 1997; Leguerrier, 2005). The LIM-MCMC therefore provided more realistic estimates of respiration at the Bay of Biscay continental shelf than the Ecopath model.

T.., calculated as the sum of all flows, represents the size of the entire system in terms of flows (Ulanowicz, 1986) and corresponds to total system activity. The nominal Ecopath value was above the range of LIM-MCMC estimates. This is probably due to (i) a lack of consideration of autopredation (cannibalism and species groups that feed on themselves) flows in the LIM-MCMC approach; (ii) natural mortality, i.e., mortality due to causes other than predation (disease, other natural causes of death), which was included in the Ecopath model, and (iii) the importance of the estimate of detritus export in the LIM-MCMC (less cycling). All these effects may have lowered system activity (and T.. value) in the LIM-MCMC, despite the fact that this model considered a higher number of interactions than the Ecopath model (e.g., additional bacterial flows and more detailed consideration of detrital processing). Internal relative ascendency (Ai/Ci) is computed with no regard for external flows (e.g., flows entering and exiting from the ecosystem) including, importantly, imports of GPP into the system. In this study the mean value of Ai/Ci ratio was 0.34 (*vs.* 0.22 for the Ecopath model). The higher Ai/Ci ratio in the LIM-MCMC suggests that the ecosystem specialization was higher if model implements additional bacterial flows (e.g., flows of bacteria consumption) and more detailed consideration of detrital processing, i.e., disaggregation of particulate and dissolved organic matter into two different compartments (e.g., egestion flows, phytoplankton exudation, or indirectly by a production by viruses and cellular lysis). This conclusion reinforces the need for better representation of bacterial loop

441 processes in ecosystem functioning, and thence the importance of including them in models
442 (Saint-Béat, 2012). In this case, the LIM-MCMC seems to be a relevant tool to do this.

443 Several authors referring to Ulanowicz (1986) proposed the use of internal relative
444 ascendency to discuss ecosystem maturity (Baird et al., 2007; Baird et al., 2009), which may
445 lead to possible mis-interpretation. Ai/Ci, CI, and SOI values from both models indicated that
446 the food chain has a web-like structure with internal flows of intermediate complexity
447 (Libralato et al., 2008). Both models produced estimates indicative of a system less mature
448 than similar ecosystems such as the Atlantic shelf or the Cantabrian Sea (Trites et al., 1999;
449 Sanchez and Olaso, 2004; López, 2010).

450 The FCI (ratio of total flow recycled to total flow through the system) estimates from LIM-
451 MCMC were lower than the Ecopath value, indicating less cycling; a finding in line with the
452 respective estimates of total system throughput. Intrinsic characteristics of ecosystem models
453 should be acknowledged when analyzing the recycling index, regarding the importance of the
454 export of detritus out of the system (sedimentation or current export) from both methods. This
455 may, at least, partly explain the difference in FCI values. As mentioned above the Ecopath
456 model was designed to consider more cycles and take into account autopredation and related
457 ontogenic changes (e.g., adults feeding on larvae of the same group of fish). These trophic
458 interactions were not integrated into the LIM-MCMC and this may have contributed to the
459 difference in FCI values. Around 10 autopredation flows described in the Ecopath model of
460 the study area were not considered in the LIM-MCMC. Inclusion of autopredation processes
461 would improve our LIM-MCMC. Differences in FCI estimates may also be explained by the
462 number of compartments (aggregation) used in the two models; it has been shown that the
463 LIM-MCMC method tends to underestimate the size and complexity of food webs (Johnson et
464 al., 2009). For estimates of some ecological network indices, the aggregation scheme
465 explained as much variability as the difference between the inverse-derived and raw flows.

466 Topological network indices tend to be fairly robust against aggregation, whereas the FCI, a
467 functional index, is very sensitive to aggregation effects. Allesina et al. (2005) and, more
468 recently, Fath et al. (2007), arrived at similar conclusions, stressing the interest of work on
469 scaled indices, including ratios such as the Ai/Ci.

470 Both models agreed on general detritivorous system functioning, with very similar estimates
471 of D/H ratio. Ecological interpretation of the D/H ratio remains controversial (Ulanowicz,
472 1992; Dame and Christian, 2007). Niquil et al. (2014a) emphasized that further research is
473 needed before the D/H ratio can be used operationally to assess the impact of disturbances on
474 the trophic state and functioning of ecosystems. Lassalle et al. (2011) related the dominance
475 of detritivory in the Bay of Biscay continental shelf food web to the Primary
476 production/Respiration ratio value, which was close to 1 and therefore characteristic of a
477 mature system in a state of organic carbon balance.

478

479 Specific recommendations for future field surveys and research emerged from work on the
480 development of this new model of the Bay of Biscay continental shelf food web. We found
481 that (a) there was no precise estimate of GPP in the study area, only model outputs; (b) there
482 were no data on export of particulate organic matter from the system, it is considered more
483 reasonable when dealing with large ecosystems to rely on expert judgments, rather than on
484 approximate data, to shrink some confidence intervals (Johnson et al., 2009); (c)
485 that vigilance is recommended when making comparisons between models, as comparison of
486 indices from the Ecopath and LIM user communities revealed differences in the definitions
487 and formulations of ENA indices. Preliminary work on translating the Ecopath routines into
488 Matlab code is currently in progress (Kearney et al., 2012); this includes work on the
489 harmonization of formulae for ENA indices (Guesnet, pers. comm.). This work will also
490 require careful comparison of the Ecopath and LIM-MCMC methods using the same number

491 of compartments and a similar number of entering and exiting flows. (ii) The use of different
492 modeling methods, and more particularly model structures (number of compartments), may
493 lead to systematic differences in results. Some differences in the estimates produced by the
494 two modeling methods could be also easily explained, for instance the CI index is known to
495 be sensitive to the number of modeling compartments and the number of interactions between
496 them (Johnson et al., 2009). The different structures of the models produced by the two
497 methods may therefore account for the observed difference in CI estimates. Such ongoing
498 research studies will make it easier to compare model outputs and thus contribute to
499 corroborating ecological conclusions derived from modeling studies and help to ensure that
500 they are translated into management strategies and practice.

501

502 The LIM-MCMC of the Bay of Biscay continental shelf appears to be in line with ICES
503 expectations. This new model was intended to provide an overview of the structural and
504 functional properties of the food web through the calculation of holistic indices compatible
505 with the revised ICES criteria and indicators adopted by the MSFD. New indices should
506 include sufficient taxonomic groups to represent the full range of taxonomic groups that make
507 up the food web in an ecosystem (ICES, 2013). Research should therefore focus on
508 developing more integrated, functional indices which capture whole-system approaches,
509 processes, linkages (e.g., connectance and recycling) and food-web dynamics and can relate
510 changes in values to anthropogenic factors (Rombouts et al., 2013). As a direct perspective of
511 use, ENA indices derived from this model should be tested through a sensitivity analysis with
512 respect to anthropogenic climate changes and direct pressures, in line with the European
513 directives and recommendations by working groups (OSPAR).

5. Conclusion

This study has presented a new modeling tool which was used to characterize the food web status and structural and functional properties of the Bay of Biscay ecosystem. A comparison with the pre-existing Ecopath model built for the same area - the continental shelf between 30 m- and 150 m-isobaths - revealed, that both approaches resulted in similar ecological conclusions with respect to food web structure and functioning. This finding was unexpected and interesting, as the two models were developed for different purposes. Ecopath with Ecosim was originally used as a tool for ecosystem-based fishery management, whereas the LIM-MCMC method was developed to provide an overview of ecosystem functioning and a description of the system in terms of its emergent properties (e.g., ENA indices). Further analysis of the few differences in estimates produced by the two approaches is required however, as some compensatory effects may have occurred. The LIM-MCMC method potentially has several advantages over the Ecopath with Ecosim approach, and may lead to practical applications not currently possible with the Ecopath software (such as a quantification of uncertainty in the flows and food-web properties), although at present the Ecopath with Ecosim method remains the most widely used dynamic-ecosystem food-web model and still offers useful specificities for ecosystem-based management such as the distinction between detritus and discards.

The main advantages of this new approach are that it enables quantification of uncertainty in the flows and food-web properties - an important gap in some previous models - and addresses the poor integration of low-trophic-level processes in some earlier models (see for instance Pinkerton et al., 2008). Data on uncertainty, including comparison with single value estimations, are of considerable interest and research to implement similar improvements in Ecopath is already under way (Lassalle et al., 2014). An inherent feature of the LIM-MCMC method is that it allows the uncertainty of field data or of experiments to be taken into account

539 in the model construction (inequalities definition) (Van den Meersche et al., 2009; van
540 Oevelen et al., 2010; Niquil et al., 2012). The level of uncertainty is also captured in the result
541 (with a range of possible values being estimated) (Van den Meersche et al., 2009; van
542 Oevelen et al., 2010; Niquil et al., 2012). Quantitative values for uncertainties can also be
543 used in statistical comparisons. In this study we were unable to compare estimates statistically
544 because of the large difference in sample sizes but estimates from two LIM-MCMCs could be
545 compared, for instance models of different ecosystems, or before and after models of an
546 ecosystem which experiences a perturbation. Some statistical tools could be used even if
547 observations were not independent (Beaugrand pers. comm.), which is not the case for LIM-
548 MCMC data owing to the Markov chain.

549 Another argument for quantification of uncertainty relates to the detection of shifts in the state
550 of an ecosystem. Recent studies of abrupt changes in marine and coastal ecosystems have
551 suggested that increasing variance is an indicator of such events (Beaugrand et al., 2008). A
552 recent study (Niquil et al., submitted) confirmed an earlier report of a climatic shift in the
553 Mediterranean Sea (Tomczak et al., 2013), and showed that ENA indices were sensitive to
554 this shift and that it affected the variability of ENA index values. Such examples confirm the
555 importance of considering the uncertainty of indices and flows. In the context of climate
556 changes, which are expected to have a large impact on biological communities, and therefore
557 their interactions and associated carbon flows (Hughes, 2000; Luczak et al., 2011), the LIM-
558 MCMC method could be used for sensitivity analysis, with constraints on specific biological
559 compartments being modified according to climatic future projections. For example, after the
560 construction of a LIM-MCMC, constraints on specific biological compartments can be easily
561 forced by outputs from niche-based models (Raybaud et al., in revision) or biogeochemical
562 models (Bopp et al., 2013) based on different climatic scenarios. Given the uncertainty of the
563 LIM-MCMC constraints provided by such tools, a model based on fixed values would be

564 unsuitable for research using such forcing. The LIM-MCMC method is also a very
565 appropriate tool to be used in this way to study human-induced impacts at an ecosystem level.
566

567 Acknowledgements

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569 for understanding marine biodiversity and assessing good Environmental Status) project
570 funded by the European Union under the 7th Framework Programme, 'The Ocean for
571 Tomorrow' Theme (grant agreement no. 308392; www.devotes-project.eu).

572 Table 1: Compartments of the LIM-MCMC of the Bay of Biscay continental shelf. Detail
573 corresponds to the compartment species composition. Abbreviation is a three-letter code that
574 is required to identify compartments in the LIM-MCMC approach.

Compartments	**Detail**	**Abbreviation and code**
Marine mammals	5 main species: the short-beaked common dolphin *Delphinus delphis*, the striped dolphin *Stenella coeruleoalba*, the bottlenose dolphin *Tursiops truncatus*, the long-finned pilot whale *Globicephala melas*, and the harbor porpoise *Phocoena phocoena*	mma; 1
Seabirds	mainly gulls, kittiwakes, gannets, and auks	sbr; 2
Cephalopods	the broadtail short-finned squid *Illex coindetii*, the European flying squid *Todarodes sagittatus*, 4 *Loliginidae* squid species , the horned octopus *Eledone cirrhosa*, the common octopus *O. vulgaris*, and species of the *Sepiidae* family	cep; 3
Pelagic piscivores	main species including the Atlantic mackerel *Scomber scombrus*, and the horse mackerel *Trachurus trachurus* and tunas (albacore tuna *Thunnus alalunga* and bluefin tuna *T. thynnus)*	pps; 4
Pelagic planktivores	3 main species considered : the European anchovy *Engraulis encrasicolus*, the European sprat *Sprattus sprattus* and the European pilchard *Sardina pilchardus*	ppl; 5
Demersal piscivores	42 species including the Conger eel *Conger conger*, the Whiting pout *Trisopterus luscus*, the lesser spotted dogfish *Scyliorhinus canicula*, and the European hake *Merluccius merluccius*	dps; 6
Demersal benthivores	group of 32 species including benthivorous and suprabenthivorous species such as the common sole *Solea solea* and the blue whiting *Micromesistius poutassou*	dbn; 7
Carnivorous/necropha-geous invertebrates	isopods (necrophageous), polychaetes, and crustacean decapods such as the Norwegian lobster *Nephrops norvegicus* (carnivorous)	cbi; 8
Benthic deposit feeders	polychaetes, sea urchins, and sea cucumbers	dep; 9
Benthic suspension feeders	mainly crustaceans and bivalves	sus; 10
Meiofauna	largely dominated by nematodes	mef; 11
Macrozooplankton	mainly composed of decapods and jelly plankton (tunicates, cnidarians)	maz; 12
Mesozooplankton	mostly of metazoans with copepods predominating	mez; 13
Microzooplankton	protozoans <200 µm, mostly ciliates and heterotrophic flagellates	miz; 14
Phytoplankton	total chlorophyll a and phytoplankton production by in situ 14C method	phy; 15
Detritus	particulate matter (including allochtonous material, feces, sedimenting matter, discards)	det; 16

Bacteria	benthic and pelagic bacteria	bac; 17
DOC	Dissolved Organic Carbon	doc; 18

575 Table 2: Aggregation differences between the Ecopath model of the Bay of Biscay continental
576 shelf (Lassalle et al., 2011) and the LIM-MCMC for the same area. The compartment code for
577 the LIM-MCMC was given with the species composition in Table 1. 'DOC' means dissolved
578 organic carbon.

579

Ecopath groups number	**Ecopath compartments**	**LIM groups aggregation**
1	Pursuit divers seabirds	1
2	Surface feeders seabirds	1
3	Striped dolphins	2
4	Bottlenose dolphins	2
5	Common dolphins	2
6	Long-finned pilot whales	2
7	Harbour porpoises	2
8	Piscivorous demersal fish	3
9	Piscivorous and benthivorous demersal fish	3 and 4
10	Suprabenthivorous demersal fish	4
11	Benthivorous demersal fish	4
12	Mackerel	5: new group of pelagic piscivorous
13	Horse mackerel	
14	Anchovy	6
15	Sardine	6
16	Sprat	6
17	Benthic cephalopods	7
18	Pelagic cephalopods	7
19	Carnivorous benthic invertebrates	8
20	Necrophagous benthic invertebrates	8
21	Sub-surface deposit feeders invertebrates	9
22	Surface suspension and deposit feeders inv.	9 and 10
23	Benthic meiofauna	11
24	Suprabenthic invertebrates	10
25	Macrozooplankton	12
26	Mesozooplankton	13
27	Microzooplankton	14
28	Bacteria	15
29	Large phytoplankton	16
30	Small phytoplankton	16
31	Discards	17
32	Detritus	17
X	X	18: new group of DOC

580

Table 3: Comparison of respiration flows estimated by the LIM-MCMC and the Ecopath model (Lassalle et al., 2011) of the Bay of Biscay continental shelf. Flow names in the LIM-MCMC were composed of the three-letter code of the compartment of origin followed by the three-letter code of the destination compartment. Mean corresponds to the mean flow value calculated from the one million simulations. Standard deviations, minimum and maximum estimates are also presented. Flows were in $kgC.km^{-2}.y^{-1}$.'*' indicated when the Ecopath estimate was comprised between the maximum and minimum LIM-MCMC estimates. The values of the respiration flows estimated by the LIM-MCMC with no direct comparison possible to Ecopath (due to aggregation bias) were in grey.

		LIM-MCMC				Ecopath	
Respiration flows	**Name**	**Mean**	**Standard deviation**	**Minimal estimate**	**Maximal estimate**	**Ecopath estimate**	**Overlap**
marine mammals	mmaTOres	30.51	23.10	0.00	214.92	87.95	*
seabirds	sbrTOres	533.44	189.58	100.84	1521.96	16.42	
cephalopods	cepTOres	82.76	57.61	0.00	425.96	29.61	*
pelagic piscivores	ppsTOres	168.45	168.43	55.00	43.08	-	-
pelagic planktivores	pplTOres	2581.47	2563.21	534.93	967.85	318.38	
demersal piscivores	dpsTOres	32.43	9.72	10.85	68.97	318.38	
demersal benthivores	dbnTOres	146.48	32.01	25.60	216.56	1250.65	
carnivorous/necropha-geous invertebrates	cbiTOres	285.73	185.02	0.00	1445.02	987.32	*
benthic suspension feeders	susTOres	563.82	199.85	33.09	1799.30	-	-
benthic deposit feeders	depTOres	441.02	176.74	26.84	1419.39	-	-
meiofauna	mefTOres	$5.78 . 10^4$	$2.61 . 10^4$	$1.76 . 10^4$	$1.15 . 10^5$	2000.00	
macrozooplankton	mazTOres	$1.67 . 10^4$	7554.99	2670.34	$4.32 . 10^4$	1999.89	
mesozooplankton	mezTOres	9279.10	2922.53	2043.44	$2.46 . 10^4$	$2.22 . 10^4$	*
microzooplankton	mizTOres	$2.41 . 10^4$	6662.49	8239.81	$4.90 . 10^4$	$1.29 . 10^5$	
phytoplankton	phyTOres	$3.44 . 10^4$	$2.63 . 10^4$	9523.87	$9.70 . 10^4$	-	-
bacteria	bacTOres	$6.17 . 10^4$	$1.93 . 10^4$	$1.89 . 10^4$	$1.04 . 10^5$	$1.94 . 10^4$	*

Table 4: System Omnivory Index (SOI) and Connectance Index (CI) estimated from the two modeling methods.

	LIM - MCMC	Ecopath model
SOI	0.19 ± 0.03	0.21
CI	0.32	0.21

598 Figure captions

599

600 Figure 1: Study area of the Bay of Biscay continental shelf and locations of the main rivers
601 flowing into it. The shaded area corresponds to the French part of the continental shelf
602 (between 30- and 150-m isobaths), and represents the spatial extent of the LIM-MCMC.

603

604 Figure 2: A. Distribution of the flow values estimated by the LIM-MCMC of the Bay of
605 Biscay continental shelf, with associated standard deviations computed on one million values
606 per flow. B. Five highest flow estimates. See Table S1 in Supplementary Material 1 for a full
607 description of flows and numerical code. 'det' is an abbreviation for particulate detritus, and
608 'doc' for dissolved organic carbon .

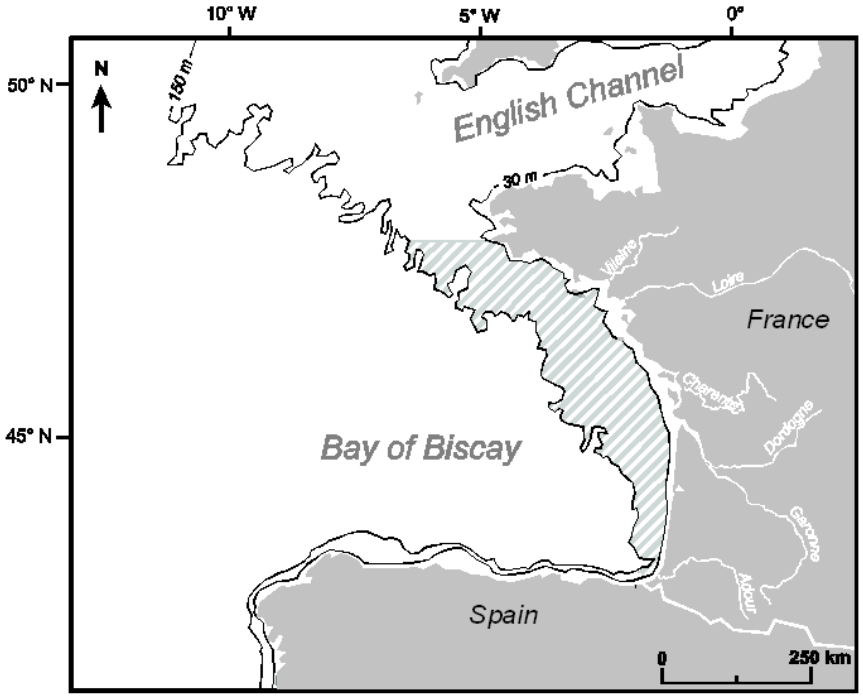
609

610 Figure 3: Input flows distribution for compartments in common between the two modeling
611 approaches. Black dots are the mean compartment throughputs estimated from one million
612 simulations of the LIM-MCMC. Minimum and maximum estimates are also shown. Red
613 triangles were the nominal values obtained from the Ecopath model. See Table 1 for
614 compartment abbreviations and Table S1 for information relative to flow estimates.

615

616 Figure 4: Estimates of Total System Throughput (T..), internal relative Ascendency (Ai/Ci),
617 Finn's Cycling Index (FCI), Detritivory on Herbivory ratio (D/H) by the two modeling
618 approaches. Black dots were the mean ENA values estimated from one million simulations of
619 the LIM-MCMC. Standard deviations are also shown. Blue and orange dots were minimum
620 and maximum estimates respectively. Red triangles were the nominal values obtained from
621 the Ecopath model.

622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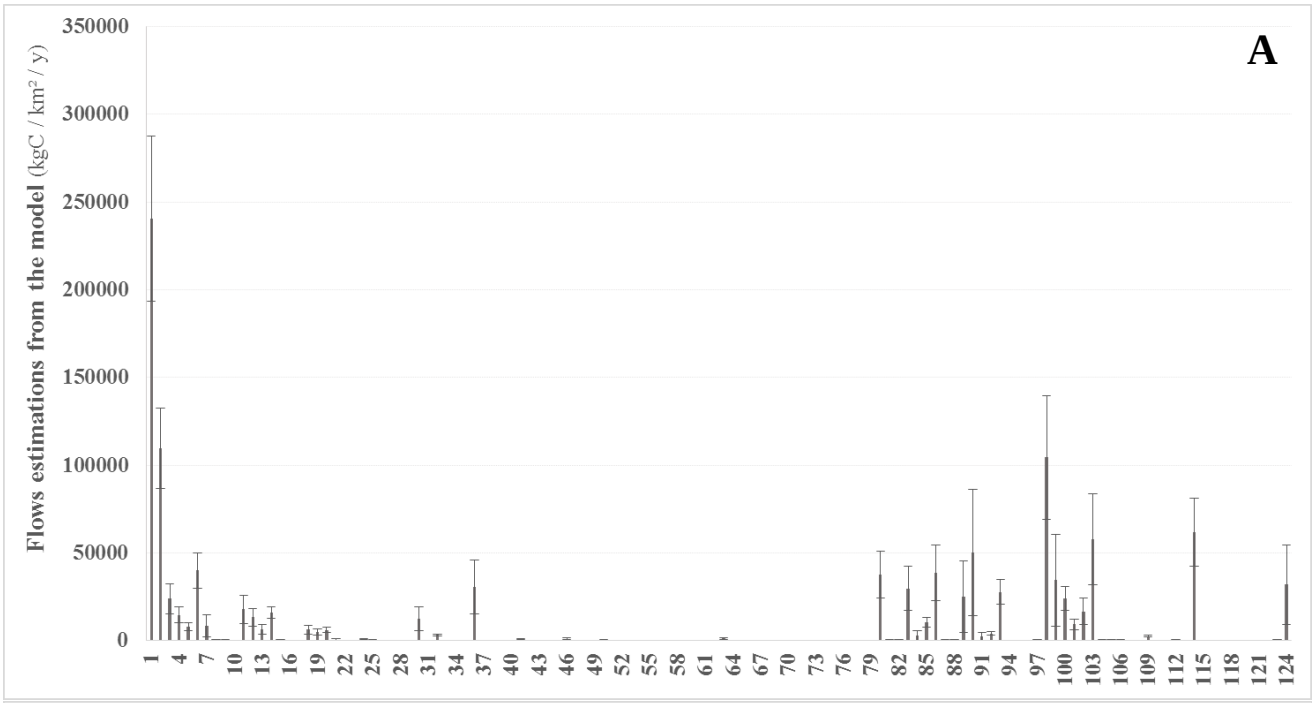
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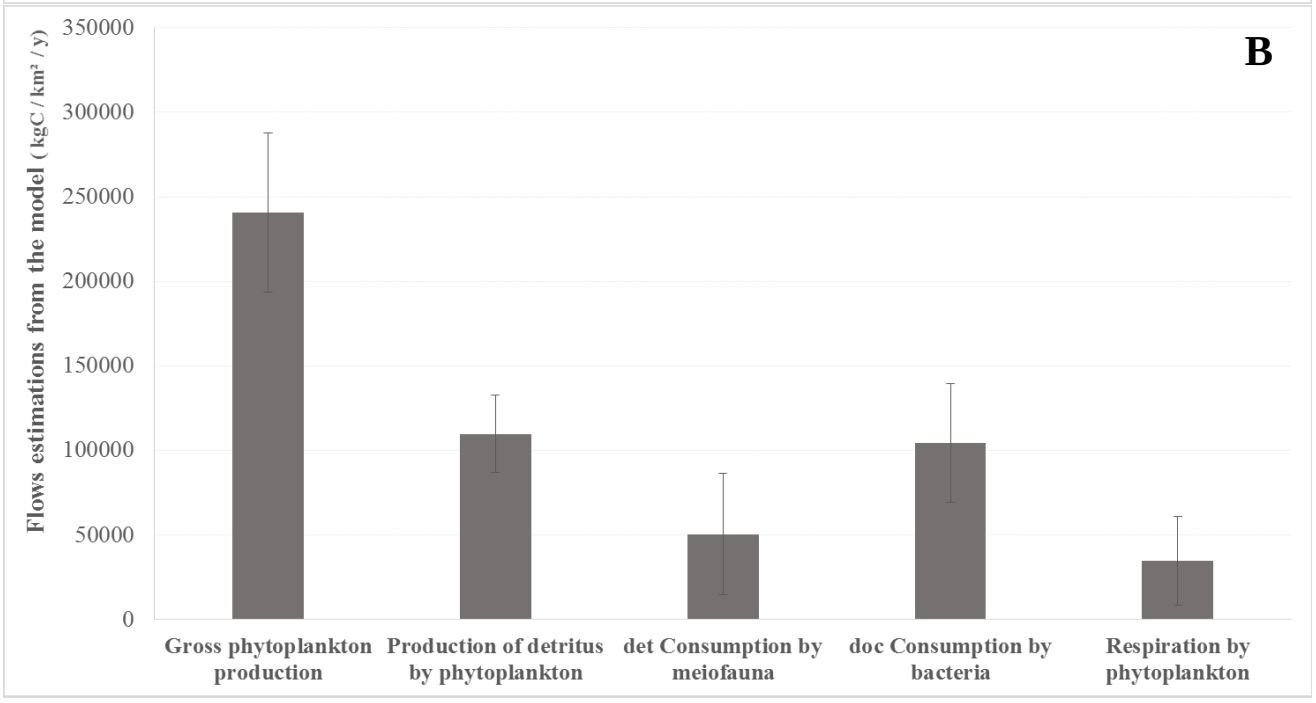
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Gross phytoplankton production
Production of detritus by phytoplankton
det Consumption by meiofauna
doc Consumption by bacteria
Respiration by phytoplankton

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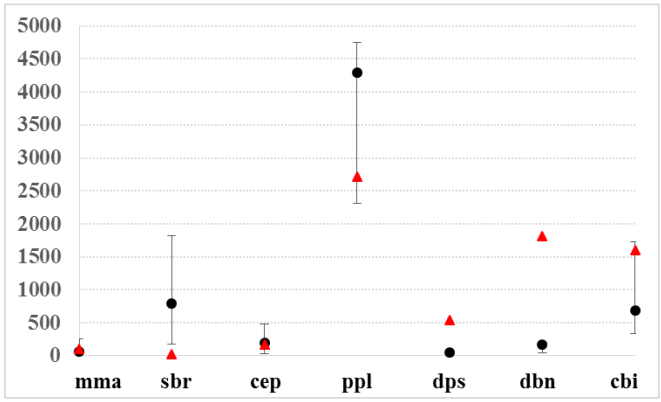
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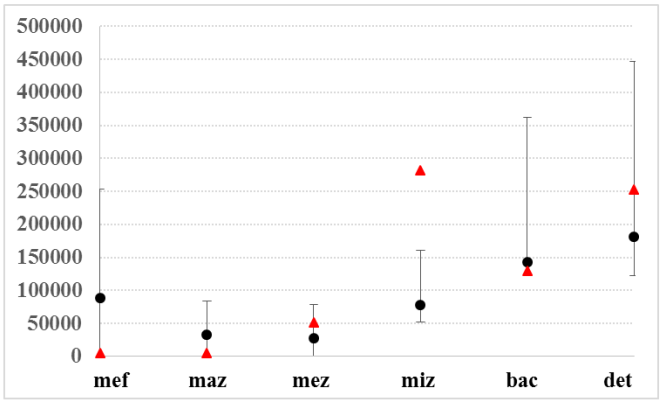
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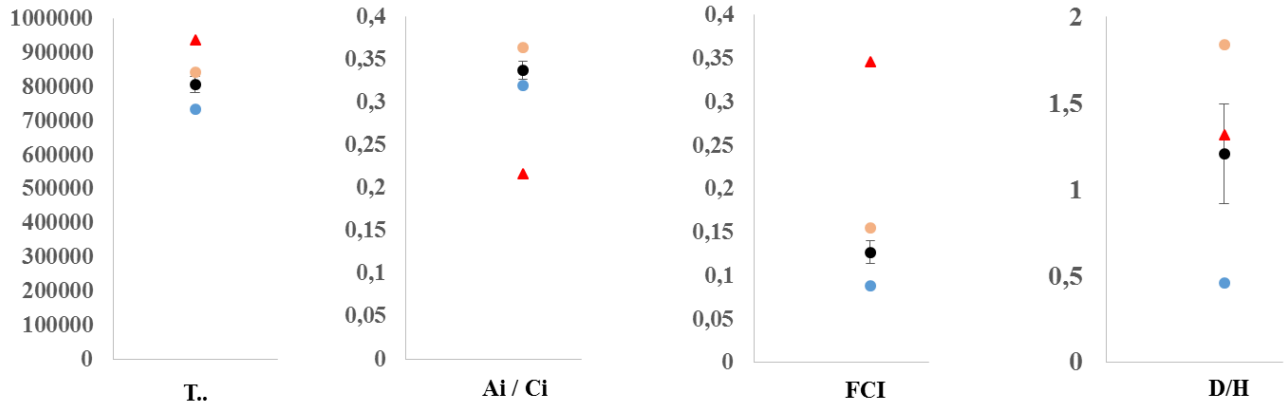
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631

632

633 Supplementary material:

634 Table S1: List of all flows ($kgC.km^{-2}.y^{-1}$) considered in the LIM-MCMC of the Bay of Biscay
635 continental shelf. Flow names are composed of the three-letter code of the compartment of
636 origin followed by the three-letter code of the destination compartment. Mean corresponds to
637 the mean flow value calculated from the 1 million simulations. The mean value is given with
638 its standard deviation.

Flow description	Abreviation	Flow number	Mean	Standard deviation
Gross phytoplankton production	gppTOphy	1	$2.41 . 10^5$	47168.65
Production of detritus by phytoplankton	phyTOdet	2	$1.10 . 10^5$	23059.88
Phytoplankton exudation	phyTOdoc	3	$2.39 . 10^4$	8572.46
Grazing of phytoplankton by macrozooplankton	phyTOmaz	4	$1.47 . 10^4$	4430.58
Grazing of phytoplankton by mesozooplankton	phyTOmez	5	8118.38	2204.63
Grazing of phytoplankton by microzooplankton	phyTOmiz	6	$4.01 . 10^4$	10057.47
Grazing of phytoplankton by meiofauna	phyTOmef	7	8567.72	6236.27
Grazing of phytoplankton by benthic deposit feeders	phyTOdep	8	556.91	277.23
Consumption of phytoplankton by benthic suspension feeders	phyTOsus	9	408.08	276.39
Consumption of phytoplankton by pelagic planktivores	phyTOppl	10	107.71	58.00
Production of detritus by microzooplankton	mizTOdet	11	$1.79 . 10^4$	8034.80
Excretion of doc by microzooplankton	mizTOdoc	12	$1.32 . 10^4$	5266.06
Grazing of microzooplankton by macrozooplankton	mizTOmaz	13	6441.45	2876.43
Grazing of microzooplankton by mesozooplankton	mizTOmez	14	$1.59. 10^4$	3444.81
Consumption of microzooplankton by suspension feeders	mizTOsus	15	358.71	334.80
Consumption of microzooplankton by pelagic planktivores	mizTOppl	16	88.26	47.59
Consumption of microzooplankton by pelagic piscivores	mizTOpps	17	17.66	6.39
Production of detritus by mesozooplankton	mezTOdet	18	6253.57	2658.35
Excretion of doc by mesozooplankton	mezTOdoc	19	4813.35	1671.46
Grazing of mesozooplankton by macrozooplankton	mezTOmaz	20	6061.94	1547.82

Consumption of mesozooplankton by suspension feeders	mezTOsus	21	474.90	417.92
Consumption of mesozooplankton by carnivorous/necrophageous invertebrates	mezTOcbi	22	72.51	19.62
Consumption of mesozooplankton by demersal benthivores	mezTOdbn	23	76.22	14.08
Consumption of mesozooplankton by pelagic planktivores	mezTOppl	24	787.22	398.29
Consumption of mesozooplankton by pelagic piscivores	mezTOpps	25	353.09	55.14
Consumption of mesozooplankton by cephalopods	mezTOcep	26	5.73	2.36
Consumption of macrozooplankton by carnivorous/necrophageous invertebrates	mazTOcbi	27	40.68	11.06
Consumption of macrozooplankton by cephalopods	mazTOcep	28	26.51	16.75
Consumption of macrozooplankton by demersal benthivores	mazTOdbn	29	38.42	9.69
Production of detritus by macrozooplankton	mazTOdet	30	$1.25 . 10^4$	6742.81
Consumption of macrozooplankton by marine mammals	mazTOmma	31	2.00	1.51
Consumption of macrozooplankton by pelagic planktivores	mazTOppl	32	3306.36	540.39
Consumption of macrozooplankton by seabirds	mazTOsbr	33	113.02	70.78
Consumption of meiofauna by carnivorous/necrophageous invertebrates	mefTOcbi	34	131.52	34.74
Consumption of meiofauna by benthic deposit feeders	mefTOdep	35	107.30	98.00
Production of detritus by meiofauna	mefTOdet	36	$3.05 . 10^4$	15458.82
Consumption of benthic deposit feeders by carnivorous/necrophageous invertebrates	depTOcbi	37	165.40	83.67
Consumption of benthic deposit feeders by cephalopods	depTOcep	38	29.87	24.28
Consumption of benthic deposit feeders by demersal benthivores	depTOdbn	39	33.87	21.98
Consumption of benthic deposit feeders by demersal piscivores	depTOdps	40	11.98	7.52
Production of detritus by benthic deposit feeders	depTOdet	41	746.02	341.29
Consumption of benthic suspension feeders by carnivorous/necrophageous invertebrates	susTOcbi	42	218.55	91.28

Consumption of benthic suspension feeders by cephalopods	susTOcep	43	30.43	24.80
Consumption of benthic suspension feeders by demersal benthivores	susTOdbn	44	34.39	22.15
Consumption of benthic suspension feeders by demersal piscivores	susTOdps	45	12.05	7.54
Production of detritus by benthic suspension feeders	susTOdet	46	990.00	406.04
Consumption of carnivorous/necrophageous invertebrates by cephalopods	cbiTOcep	47	26.93	14.69
Consumption of carnivorous/necrophageous invertebrates by demersal benthivores	cbiTOdbn	48	57.93	14.06
Consumption of carnivorous/necrophageous invertebrates by demersal piscivores	cbiTOdps	49	24.83	5.54
Production of detritus by carnivorous/necrophageous invertebrates	cbiTOdet	50	287.92	185.25
Consumption of carnivorous/necrophageous invertebrates by pelagic piscivores	cbiTOpps	51	7.98	2.22
Consumption of demersal benthivores by carnivorous/necrophageous invertebrates	dbnTOcbi	52	2.58	0.51
Consumption of demersal benthivores by cephalopods	dbnTOcep	53	0.17	0.17
Production of detritus by demersal benthivores	dbnTOdet	54	74.35	29.35
Consumption of demersal benthivores by demersal piscivores	dbnTOdps	55	5.11	0.48
Consumption of demersal benthivores by pelagic piscivores	dbnTOpps	56	2.51	0.38
Consumption of demersal benthivores by marine mammals	dbnTOmma	57	0.17	0.17
Consumption of demersal benthivores by seabirds	dbnTOsbr	58	0.15	0.14
Production of detritus by demersal piscivores	dpsTOdet	59	23.63	9.41
Consumption of demersal piscivores by cephalopods	dpsTOcep	60	6.88	1.85
Consumption of demersal piscivores by marine mammals	dpsTOmma	61	4.21	1.69
Consumption of pelagic planktivores by cephalopods	pplTOcep	62	34.51	14.30
Production of detritus by pelagic planktivores	pplTOdet	63	1272.92	504.55
Consumption of pelagic planktivores by demersal piscivores	pplTOdps	64	22.09	6.55

Consumption of pelagic planktivores by marine mammals	pplTOmma	65	35.67	18.90
Consumption of pelagic planktivores by pelagic piscivores	pplTOpps	66	9.39	3.48
Consumption of pelagic planktivores by seabirds	pplTOsbr	67	328.27	32.09
Consumption of pelagic piscivores by cephalopods	ppsTOcep	68	33.90	10.09
Production of detritus by pelagic piscivores	ppsTOdet	69	118.25	49.58
Consumption of pelagic piscivores by marine mammals	ppsTOmma	70	8.88	6.10
Consumption of pelagic piscivores by seabirds	CppsTOsbr	71	33.50	12.97
Consumption of cephalopods by carnivorous/necrophageous invertebrates	cepTOcbi	72	6.22	1.68
Consumption of cephalopods by demersal benthivores	cepTOdbn	73	2.87	1.31
Production of detritus by cephalopods	cepTOdet	74	83.05	57.70
Consumption of cephalopods by demersal piscivores	cepTOdps	75	1.18	0.30
Consumption of cephalopods by marine mammals	cepTOmma	76	10.14	7.31
Consumption of cephalopods by pelagic piscivores	cepTOpps	77	3.33	1.37
Production of detritus by seabirds	sbrTOdet	78	258.16	102.64
Production of detritus by marine mammals	mmaTOdet	79	30.56	23.16
Production of doc by bacteria	bacTOdoc	80	$3.75 . 10^4$	13318.44
Consumption of bacteria by benthic deposit feeders	bacTOdep	81	357.12	326.60
Consumption of bacteria by benthic suspension feeders	bacTOsus	82	336.28	313.82
Consumption of bacteria by meiofauna	bacTOmef	83	$2.97 . 10^4$	12463.49
Consumption of bacteria by macrozooplankton	bacTOmaz	84	2984.05	2682.27
Consumption of bacteria by microzooplankton	bacTOmiz	85	$1.03 . 10^4$	2712.86
Detritus consumption by bateria	detTObac	86	$3.85 . 10^4$	15847.09
Detritus consumption by deposit feeders	detTOdep	87	406.83	211.00
Detritus consumption by suspension feeders	detTOsus	88	271.68	192.76
Detritus dissolution	detTOdoc	89	$2.50 . 10^4$	20519.47
Detritus consumption by meiofauna	detTOmef	90	$5.03 . 10^4$	35910.84
Detritus consumption by macrozooplankton	detTOmaz	91	2505.62	2269.69
Detritus consumption by mesozooplankton	detTOmez	92	4119.58	1079.91

Detritus consumption by microzooplankton	detTOmiz	93	$2.77 . 10^4$	6982.95
Detritus consumption by carnivorous/necrophageous invertebrates	detTOcbi	94	57.48	35.70
Detritus consumption by demersal benthivores	detTOdbn	95	4.08	1.61
Detritus consumption by demersal piscivores	detTOdps	96	1.58	0.40
Detritus consumption by seabirds	detTOsbr	97	316.66	173.96
Doc consumption by bacteria	docTObac	98	$1.04 . 10^5$	35129.15
Respiration by phytoplankton	phyTOres	99	$3.44 . 10^4$	26328.44
Respiration by microzooplankton	mizTOres	100	$2.41 . 10^4$	6662.49
Respiration by mesozooplankton	mezTOres	101	9279.10	2922.53
Respiration by macrozooplankton	mazTOres	102	$1.67 . 10^4$	7554.99
Respiration by meiofauna	mefTOres	103	$5.78 . 10^4$	26096.67
Respiration by benthic deposit feeders	depTOres	104	441.02	176.74
Respiration by benthic suspension feeders	susTOres	105	563.82	199.85
Respiration by carnivorous/necrophageous invertebrates	cbiTOres	106	285.73	185.02
Respiration by demersal benthivores	dbnTOres	107	146.48	32.01
Respiration by demersal piscivores	dpsTOres	108	32.43	9.72
Respiration by pelagic planktivores	pplTOres	109	2563.21	534.93
Respiration by pelagic piscivores	ppsTOres	110	168.43	55.00
Respiration by cephalopods	cepTOres	111	82.76	57.61
Respiration by seabirds	sbrTOres	112	533.44	189.58
Respiration by marine mammals	mmaTOres	113	30.51	23.10
Respiration by bacteria	bacTOres	114	$6.17 . 10^4$	19293.67
Export of benthic deposit feeders	depTOexp	115	0.02	0.01
Export of benthic suspension feeders	susTOexp	116	0.41	0.22
Export of carnivorous/necrophageous invertebrates	cbiTOexp	117	3.61	1.93
Export of demersal benthivores	dbnTOexp	118	16.27	0.14
Export of demersal piscivores	dpsTOexp	119	11.67	0.86
Export of pelagic planktivores	pplTOexp	120	23.50	4.04
Export of pelagic piscivores	ppsTOexp	121	31.01	9.89
Export of cephalopods	cepTOexp	122	5.37	1.64
Import of detritus	impTOdet	123	502.65	262.80

Export of detritus	detTOexp	124	$3.20 . 10^{4}$	22556.17

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641 Table S2: Mass-balance equation of the LIM-MCMC of the Bay of Biscay continental shelf.

642 Flow names are composed of the three-letter code and number of the compartment of origin

643 followed by the three-letter code of the destination compartment.

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Compartments (abbreviation ; number)	Mass balances
Marine mammals (mma ; 1)	(mmaTOdet + mmaTOres) - (mazTOmma + dbnTOmma + dpsTOmma + pplTOmma + ppsTOmma + cepTOmma) = 0
Seabirds (sbr ; 2)	(sbrTOdet + sbrTOres) - (detTOsbr + mazTOsbr + dbnTOsbr + pplTOsbr + ppsTOsbr) = 0
Cephalopods (cep ; 3)	(cepTOcbi + cepTOdbn + cepTOdps + cepTOpps + cepTOmma + cepTOdet + cepTOres + cepTOexp) - (mezTOcep + mazTOcep + susTOcep + depTOcep + cbiTOcep + dbnTOcep + dpsTOcep + pplTOcep + ppsTOcep) = 0
Pelagic piscivores (pps ; 4)	(ppsTOcep + ppsTOsbr + ppsTOmma + ppsTOdet + ppsTOres + ppsTOexp) - (mizTOpps + mezTOpps + cbiTOpps + dbnTOpps + cepTOpps + pplTOpps) = 0
Pelagic planktivores (ppl ; 5)	(pplTOpps + pplTOdps + pplTOcep + pplTOsbr + pplTOmma + pplTOdet + pplTOres + pplTOexp) – (phyTOppl + mizTOppl + mezTOppl + mazTOppl) = 0
Demersal piscivores (dps ; 6)	(dpsTOcep + dpsTOmma + dpsTOdet + dpsTOres + dpsTOexp) - (detTOdps + susTOdps + depTOdps + cbiTOdps + dbnTOdps + pplTOdps + cepTOdps) = 0
Demersal benthivores (dbn ; 7)	(dbnTOcbi + dbnTOdps + dbnTOpps + dbnTOcep + dbnTOsbr + dbnTOmma + dbnTOdet + dbnTOres + dbnTOexp) - (detTOdbn + mezTOdbn + mazTOdbn + susTOdbn + depTOdbn + cbiTOdbn + cepTOdbn) = 0
Carnivorous/necrophageous invertebrates (cbi ; 8)	(cbiTOdbn + cbiTOdps + cbiTOpps + cbiTOcep + cbiTOdet + cbiTOres + cbiTOexp) - (detTOcbi + mezTOcbi + mazTOcbi + mefTOcbi + susTOcbi + depTOcbi + dbnTOcbi + cepTOcbi) = 0
Benthic deposit feeders (dep ; 9)	(depTOcbi + depTOdbn + depTOdps + depTOcep + depTOdet + depTOres + depTOexp) - (phyTOdep + detTOdep + bacTOsus + mefTOdep) = 0
Benthic suspension feeders (sus ; 10)	(susTOcbi + susTOdbn + susTOdps + susTOcep + susTOdet + susTOres + susTOexp) - (phyTOsus + mizTOsus + mezTOsus + detTOsus + bacTOsus) = 0
Meiofauna (mef ; 11)	(mefTOcbi + mefTOdep + mefTOdet + mefTOres) - (phyTOmef + detTOmef + bacTOmef) = 0
Macrozooplankton (maz ; 12)	(mazTOcbi + mazTOdbn + mazTOppl + mazTOcep + mazTOsbr + mazTOmma + mazTOdet + mazTOres) - (phyTOmaz + detTOmaz + bacTOmaz + mizTOmaz + mezTOmaz) = 0
Mesozooplankton (mez ; 13)	(mezTOdet + mezTOdoc + mezTOmaz + mezTOsus + mezTOcbi + mezTOdbn + mezTOppl + mezTOpps +

	mezTOcep + mizTOres) - (phyTOmez + detTOmez + mizTOmez) = 0
Microzooplankton (miz ; 14)	(mizTOdet + mizTOdoc + mizTOmez + mizTOmaz + mizTOsus + mizTOppl + mizTOpps + mizTOres) - (phyTOmiz + detTOmiz + bacTOmiz) = 0
Bacteria (bac ; 15)	(bacTOmiz + bacTOmaz + bacTOmef + bacTOsus + bacTOdep + bacTOdoc + bacTOres) - (detTObac + docTObac) = 0
Phytoplankton (phy ; 16)	(phyTOdet + phyTOdoc + phyTOmiz + phyTOmez + phyTOmaz + phyTOmef + phyTOdep + phyTOsus + phyTOppl + phyTOres) – (gppTOphy) = 0
Detritus (det ; 17)	(detTOmiz + detTOmez + detTOmaz + detTOmef + detTOsus + detTOdep + detTOcbi + detTOdbn + detTOdps + detTOsbr + detTObac + detTOdoc + detTOexp) - (impTOdet + phyTOdet + mizTOdet + mezTOdet + mazTOdet + mefTOdet + susTOdet + depTOdet + cbiTOdet + dbnTOdet + dpsTOdet + pplTOdet + ppsTOdet + cepTOdet + sbrTOdet + mmaTOdet) = 0
Dissolved Organic Carbon (doc ; 18)	(docTObac) - (phyTOdoc + mizTOdoc + mezTOdoc + bacTOdoc + detTOdoc) = 0

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Table S3: Constraints description, with 'GPP' for gross primary production, 'R' for respiration, 'Ex' for excretion, 'Det' for the loss to the detritus, 'Ing' for the total ingestion (sum of all consumptions), and 'NPP' for net primary production.

Respiration	**Lower limit**	**Upper limit**	**References**
Bacteria	50 % of doc ingestion by bacteria	75 % of doc ingestion by bacteria	Vézina and Savenkoff, 1999
Phytoplankton	5 % of GPP	30 % of GPP	Vézina and Platt, 1988
Microzooplankton	20 % of ingestion	R + Ex + Det < 0.75 • Ing	Vézina and Savenkoff, 1999; Breed et al., 2004
Mesozooplankton	20 % of ingestion	R + Ex + Det < 0.75 • Ing	Breed et al., 2004
Macrozooplankton	20 % of ingestion	N.A.	Vézina and Savenkoff, 1999
Meiofauna	N.A.	-0.5 • Ing + 0.5 • Loss to det	van Oevelen et al., 2006
Suspension feeders	0.7 • (Ing - Loss to det)	-0.3 • Ing + 0.3 • Loss to det	van Oevelen et al., 2006
Deposit feeders	0.7 • (Ing - Loss to det)	-0.3 • Ing + 0.3 x Loss to det	van Oevelen et al., 2006

Excretion			
Phytoplankton	10 % of NPP ; 5 % of GPP	30 % of NPP ; 50 % of GPP	Vézina and Platt, 1988; Vézina and Savenkoff, 1999
Microzooplankton	10 % of ingestion ; 33 % of respiration	100 % of respiration	Vézina and Platt, 1988
Mesozooplankton	10 % of ingestion	100 % of respiration	Vézina and Platt, 1988

Assimilation efficiency

Microzooplankton	AE = 50 %; 0.5 • Ing	AE = 90 % ; 0.1 • Ing	Vézina and Platt, 1988
Mesozooplankton	AE = 50 %; 0.5 • Ing	AE = 90 % ; 0.1 • Ing	Vézina and Platt, 1988
Suspension feeders	AE = 57 %; 0.43 • Ing	AE = 77 %; 0.23 • Ing	van Oevelen et al., 2006
Deposit feeders	AE = 40 %; 0,6 • Ing	AE = 75 % ; 0,25 • Ing	van Oevelen et al., 2006
Carnivorous/ necrophageous inverteb.	AE = 40 %; 0,6 • Ing	AE = 75 % ; 0,25 • Ing	van Oevelen et al., 2006
Demersal benthivores	AE = 50 %; 0.5 • Ing	AE = 90 % ; 0.1 • Ing	Leguerrier et al., 2004
Demersal piscivores	AE = 50 %; 0.5 • Ing	AE = 90 % ; 0.1 • Ing	Leguerrier et al., 2004
Pelagic planktivores	AE = 50 %; 0.5 • Ing	AE = 90 % ; 0.1 • Ing	Leguerrier et al., 2004
Pelagic piscivores	AE = 50 %; 0.5 • Ing	AE = 90 % ; 0.1 • Ing	Leguerrier et al., 2004
Seabirds	AE = 0.43 (herb. birds) ; 0.56 • Ing	AE = 0.8 (carn. birds); 0.2 • Ing	Scheiffart and Nehls, 1997

Growth efficiency

Mesozooplankton	GE = 0.50	GE = 0.75	Christensen and Pauly, 1992
Macrozooplankton	GE = 0.7	GE = 0.9	Christensen and Pauly, 1992

Suspension feeders	GE = 0.7	GE = 0.91	Christensen and Pauly, 1992
Deposit feeders	GE = 0.7	GE = 0.91	Christensen and Pauly, 1992
Carnivorous/ necrophageous inverteb.	GE = 0.70	GE = 0.90	Winberg, 1956
Demersal benthivores	GE = 0.70	GE = 0.90	Winberg, 1956
Demersal piscivores	GE = 0.70	GE = 0.90	Winberg, 1956
Pelagic planktivores	GE = 0.70	GE = 0.90	Winberg, 1956
Pelagic piscivores	GE = 0.70	GE = 0.90	Winberg, 1956

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